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A living fossil *Waikalasma boucheti* n.sp. (Cirripedia, Balanomorpha) from Vanuatu (New Hebrides), Southwest Pacific

by John S. BUCKERIDGE

Abstract. — This paper describes *Waikalasma boucheti* n.sp., the first known living representative of the Eolasmatinae, a cirripede subfamily previously known only from the Palaeocene-Miocene of Australasia. The present material, recovered from the bathyal environment off Vanuatu, strengthens the case for *Waikalasma* being considered as the outgroup of all modern acorn barnacles, and provides further evidence to confirm the Eolasmatinae as one of the most primitive groups of the Balanomorpha.

Key-words. — *Waikalasma boucheti*, Eolasmatinae, Balanomorpha, Cirripedia, Vanuatu, Southwest Pacific.

Découverte d'une balane, fossile vivant, *Waikalasma boucheti* n.sp. (Cirripedia, Balanomorpha) aux Vanuatu (Nouvelles-Hébrides), sud-ouest Pacifique.

Résumé. — Cet article décrit *Waikalasma boucheti* n.sp., première espèce vivante des Eolasmatinae, une sous-famille de cirripèdes seulement connue du Paléocène-Miocène d'Australasie. Ce matériel, découvert dans un faciès bathyal au large de Vanuatu, confirme le fait que *Waikalasma* est un groupe extérieur des cirripèdes balanes et fournit une autre évidence que les Eolasmatinae sont l'un des groupes les plus primitifs des Balanomorpha.

Mots-clés. — *Waikalasma boucheti*, Eolasmatinae, Balanomorpha, Cirripedia, Vanuatu, sud-ouest Pacifique.

J. S. BUCKERIDGE, *Department of Civil and Environmental Engineering, UNITEC, Private Bag 92025, Auckland, New Zealand*

INTRODUCTION

The first known species of *Waikalasma* was described as a fossil by BUCKERIDGE (1983), from the early Miocene Waikawau cast beds of Port Waikato, New Zealand. The genus is significant in that it possesses eight plates in the shell wall and is surrounded by two or more rows of smaller, imbricating plates. These characters are considered primitive (BUCKERIDGE 1983), and place *Waikalasma* not only early, but central in the phylogeny of the Balanomorpha (BUCKERIDGE & NEWMAN 1992; NEWMAN & YAMAGUCHI 1995; BUCKERIDGE 1996). The specimens described in this paper were collected either by a Waren dredge (DW), or beam trawl (CP), from waters near Vanuatu as part of the MUSORSTOM 8 (1994) expedition. Both specimens were recovered from what appears to have been a rocky substrate.

The barnacles are preserved in alcohol, and have been examined with the aid of light microscopy and dissection. In addition to photographs of the exterior of both holotype and paratype,

illustrations of the whole animal, shell and appendages, have been drawn with the aid of a camera lucida.

The holotype MNHN-Ci2428 and the paratype MNHN-Ci2506, have been deposited in the Muséum national d'Histoire naturelle (MNHN), Paris, France.

SYSTEMATIC PART

Family PACHYLASMATIDAE Utinomi, 1968
Subfamily EOLASMATINAE Buckeridge, 1983

DIAGNOSIS (emend.). — Shell of eight distinct compartmental plates, rostrolatera not entering sheath, second carinolatera barely entering sheath; basis membranous.

DISTRIBUTION (emend.). — Upper Palæocene to Lower Miocene (New Zealand), Lower Miocene (Victoria, Australia); Recent, 700-850 m (off Vanuatu).

DISCUSSION

When originally erected, this subfamily comprised two monotypic genera, represented by *Eolasma maxwelli* Buckeridge, 1983 (Lower Palæocene, New Zealand) and *Waikalasma juneae* Buckeridge, 1983 (Lower Miocene, New Zealand). Since then, the geographic distribution has been extended to the Miocene of Victoria, Australia, by *Eolasma rugosa* Buckeridge, 1985 and is now known from the Recent in seas off Vanuatu (previously known as the New Hebrides). Initially it was thought that there were no imbricating plates present, but close examination of the holotype of *Waikalasma juneae* demonstrated the remains of at least two whorls of small imbricating plates (BUCKERIDGE & NEWMAN 1992). In the same paper, following YAMAGUCHI & NEWMAN (1990), a new interpretation of capitular plate arrangement in *Waikalasma* was provided. It is this interpretation, of rostrum-rostrolatus-carinolatus-second carinolatus-carina (RRL-CL-CL_2-C), that is adopted here.

Genus **WAIKALASMA** Buckeridge, 1983

DIAGNOSIS (emend.). — Shell bilaterally symmetrical with eight solid, calcareous, weakly articulated compartmental plates, including very wide carina (C), moderately narrow rostrum (R), and narrower, paired rostrolatera (RL), carinolatera (CL) and second carinolatera (CL_2); alae well developed, particularly on carina, but almost confluent with paries; radii absent; with two or more whorls of imbricating plates; basis membranous; caudal appendages absent.

DISTRIBUTION (emend.). — Lower Miocene to Recent. Oceania.

TYPE SPECIES. — *Waikalasma juneae* Buckeridge, 1983. Miocene (Aquitanian), Port Waikato, New Zealand.

Discussion

The origin of the Balanomorpha is within the Brachylepadomorpha, and a clear lineage can be deduced with *Waikalasma* and *Eochionelasmus* placed at the earliest stages of balanomorph radiation (Buckeridge & Newman 1992; Newman & Yamaguchi 1995). However, the hard parts of *Waikalasma* differ primarily from a *Neobrachylepas* form in only two ways: the loss of median latera, and the adoption of a configuration whereby imbricating plates are added to the shell from outside the preceding whorl. The soft parts of *Waikalasma* are quite distinct from those of *Neobrachylepas*, which are rather unusual and have been interpreted as adaptations to feeding (Newman & Yamaguchi 1995). The structural arrangement of *Waikalasma* represents a grade of organisation between balanomorphs with three pairs of partially and fully integrated latera, and also between those with numerous whorls of basal imbricating plates and those with none.

Waikalasma boucheti n.sp.
(Figs 1a-f; 2a-g; 3a-h; 4a, b)

Material examined. — Vanuatu, MUSORSTOM 8: stn CP 1080, 15°57'S – 167°27'E, 799-850 m, 5.X.1994, 1 specimen (holotype); stn DW 1113, 14°53'S – 167°06'E, 700-736 m, 8.X.1994, 1 specimen (paratype).

Etymology. — The new species is named for Philippe Bouchet, Muséum national d'Histoire naturelle, Paris. Dr Bouchet was one of the principal scientists on the 1994 MUSORSTOM expedition.

Habitat. — Station CP 1080 was situated eleven kilometres off the north east coast of île Malekula. The barnacle was attached to a brown, weathered, tuffaceous sandstone, the broken surface of which suggests that this may have been an outcrop rather than a large pebble. Associated fauna at this site was rich, including teleosts, scaphopods, gastropods and other crustaceans. The specimen from stn DW 1113 was recovered from nine kilometres off the north east cape of île Santo, attached to a large pebble of fossiliferous sandy tuff. Both areas are characterised by expanses of both rocky (predominantly basaltic) and muddy bottoms. A full account of substrate and conditions is provided in Richer de Forges *et al.* (1996).

Diagnosis

Waikalasma with two or more whorls of large imbricating plates, inner whorl with total of eight plates; scutum triangular and very elongate with long, low articular ridge, adductor muscle scar weak, central; tergum narrow, inverted "V-shaped", with deeply excavated basal margin; spur at basiscutal angle.

Description

Holotype (MNHN-Ci2428): rostro-carinal diameter 30.7 mm; width 32.5 mm; height 24.7 mm. Base membranous.

Paratype (MNHN-Ci2506): rostro-carinal diameter 26.2 mm; width 23.2 mm; height 12.8 mm.

Carina well developed, semi-conic, with extended alae, approximately 1.5 times height of rostrum. Lateral plates approximate, separated by very narrow alar zones, RL and CL_2 clearly separated from paries of rostrum and carina respectively by broad exposed alar areas on latter plates. Internally, RL not entering the sheath, CL_2 only slightly, extending into sheath as very

narrow zone of less than 1 mm wide; RL exposed for approximately 70 % of distance between basal margin and sheath, being otherwise overlapped by CL. All plates transversely sculptured with fine growth lines, each lateral plate with central, very weakly developed longitudinal rib. On most plates, growth lines with slight basal deflection approaching rib. Carina, with three similar, but less clearly defined ribs. Basally ribs approximately aligned with edges of first whorl of imbricating plates. Alae almost confluent with paries, possessing fine apico-basal striae transversely cutting well formed growth lines, latter slightly inflected at alar margin, welting absent. Holotype with imbricating plates arranged in two whorls with eight plates in each; inner plates larger, up to 6.3 mm high and 9.4 mm wide, and placed to overlap area of abutment of compartmental plates, inner whorl of imbricating plates in turn overlapped by outer whorl of plates of up to 1.7 mm height (Fig. 1f); imbricating plates develop "alar extensions" about 1 mm wide on overlapped margins; both whorls of imbricating plates closely approximate basally, forming 3.2 mm thick skirt of laminae, angling inwards to outer edge of the compartmental plates. Skirt, and base of compartmental plates in contact with substrate. Imbricating plates grow by addition of laminae from base, with outermost plates newest; laminae of both first and second whorls confluent, although in holotype, plates in outer whorl (= earliest) lack laminae.

Opercula

Tergum narrow, inverted "V-shaped", basal margin deeply excavated; apico-basal ridge broadly concave towards carina, basally becoming full width of projected basal angle; articular ridge low, quadrangular; interior lacking adductor muscle scars or furrows; exterior with well developed transverse growth lines on apico-basal and articular ridges. Scutum elongate, triangular, occludent margin 2.6 times length of basal margin; internally with very weakly developed, centrally placed, adductor muscle pit; articular ridge low, about half length of gently concave articular margin; exterior with well developed transverse growth lines, crossed by weak longitudinal striae.

Soft parts

Mandible tridentate, lower angle accuminate with two groups of short spines; first maxilla with two large and three small upper spines, notch poorly developed, centrally with group of five large spines, lower angle with three medium spines, relatively hirsute overall. Penis rudimentary, without basidorsal point. Labrum gently curved, with two or three small teeth on each side near palps, and very finely denticulated surfaces lower on either side. Palps well separated, rounded, with setae on both inner and outer sides. No eggs or branchiae were noted.

Cirri

Cirri I and II with anterior rami with one segment fewer than posterior rami. Cirrus II more like cirrus III than cirrus I. Anterior rami of cirri III, V and VI with two or three more segments than posterior rami. Cirrus IV with anterior rami longer than posterior, but appendage may have been damaged. Cirrus VI with four pairs of large setae on anterior margin of intermediate segments. Segment count per ramus as follows (anterior, posterior):

I	II	III	IV	V	VI
14, 15	24, 25	29, 32	31, 29	31, 34	29, 31

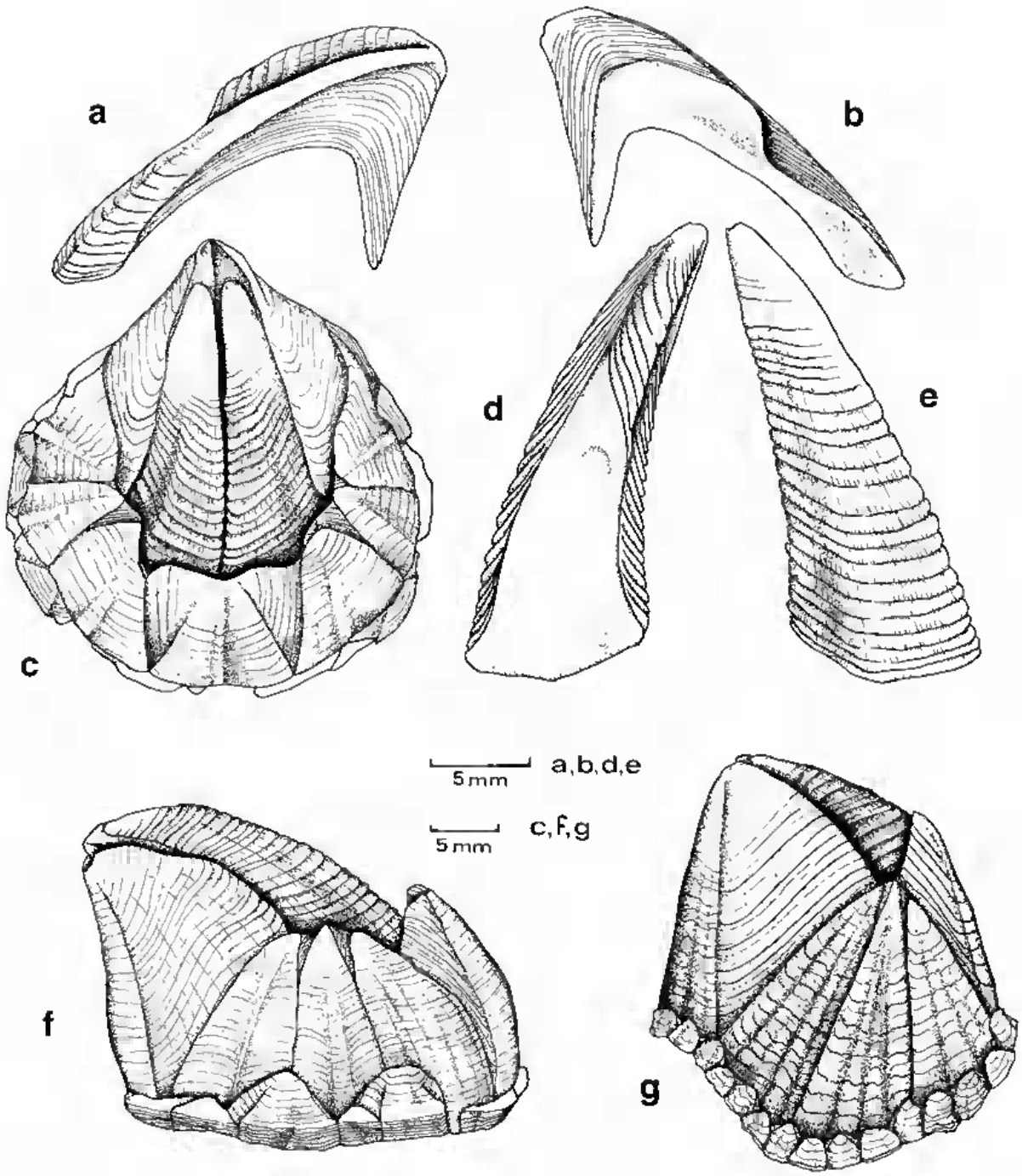

FIG. 1. — Eolasmatinae. a-f, *Waikalasma bouchet* n.sp. Holotype, MNHN-Cr2428. a, tergum (right), exterior; b, same, interior; c, dorsal view of whole specimen; d, scutum (left), interior; e, same, exterior; f, lateral view of whole specimen (left side); g, *Waikalasma juneae* Buckeridge, 1983, lateral view of whole specimen (left side), reconstruction to show placement of opercula and imbricating plates.

Colour (in alcohol)

The holotype shell is creamy-white internally and externally stained a dark brownish yellow. The paratype is cream both internally and externally. Soft tissue in the holotype has a strong purple tint, particularly on the cirri.

REMARKS

The paratype, although smaller, possesses a total of twenty-seven imbricating plates. These may be recognised as an inner whorl of eight plates, each overlapping a suture in the compartmental wall, a second whorl of twelve plates (variously interleaved and overlapping), a third whorl of six plates (generally overlapping) and a fourth whorl of one plate (Fig. 2f). The plates are smaller than in the holotype, with only one being over 5 mm in height. From the structure of the paratype it is easy to see how new plates are added to the outer imbricating whorl(s): addition is not regular, being accomplished either by interleaving with, or overlapping of, adjacent plates. At the base of the carina, (the region of greatest compartmental growth), plates are first interleaved, then placed to overlap (Fig. 4b). This pattern is essentially the same as that observed in shell compartmental growth: a primary wall of four plates (R-CL-C-CL) is enlarged by replication of the CL to produce the CL_2, which is interleaved between the C and CL; this is followed by addition of the RL, which overlaps both R and CL (see Fig. 4).

In the holotype, both opercula show significant wear in the apical regions, with the tergum this "smoothed area" extends for more than half the length of the apico-basal ridge; with the scutum, wear is confined to the upper third of the occludent margin.

The absence of caudal appendages in *W. boucheti* is intriguing, as these would have strengthened the status of *Waikalasma* as an excellent outgroup for the Pachylasmatinae. But caudal appendages, as are found in *Pachylasma*, are considered to be plesiomorphic. Natural processes however, are notably irregular, and this is certainly observed in sessilian phylogeny, where clear linear relationships, confirmed by sequential loss of pleisiomorphies, are rarely found (BUCKERIDGE 1996). The presence of a rudimentary penis may indicate the possibility of this species possessing complemental males, none were observed.

The discovery of two specimens of an extant *Waikalasma* species provides an opportunity to confirm a number of unusual characteristics that previously defined a unique, intact, but fossilized, specimen of *Waikalasma juneae*. In particular, the tight grouping of the lateral plates, with very little space between RL, CL and CL_2 is confirmed. Further, it is clear that the RL does not enter the sheath. Although the latter character was suspected in the fossil material, the fragility of that specimen prevented excavation of sediment from the interior to confirm this. Unfortunately both specimens of *W. boucheti* are adults, so do not provide conclusive evidence of the manner in which the lateral plates are added, *i.e.* during ontogeny, is the CL_2 intercalated into the wall as in higher balanomorphs? This is certainly something additional specimens may be able to clarify.

Waikalasma boucheti n.sp. (Fig. 1a-f), may be distinguished from *W. juneae* (Fig. 1g), by possessing proportionately shorter and clearly rostrally directed lateral plates. NEWMAN (pers. comm.) now considers that *W. juneae* probably had about thirty imbricating plates, possibly arranged in two whorls. His conclusion is based on the ribs or groves in the compartmental

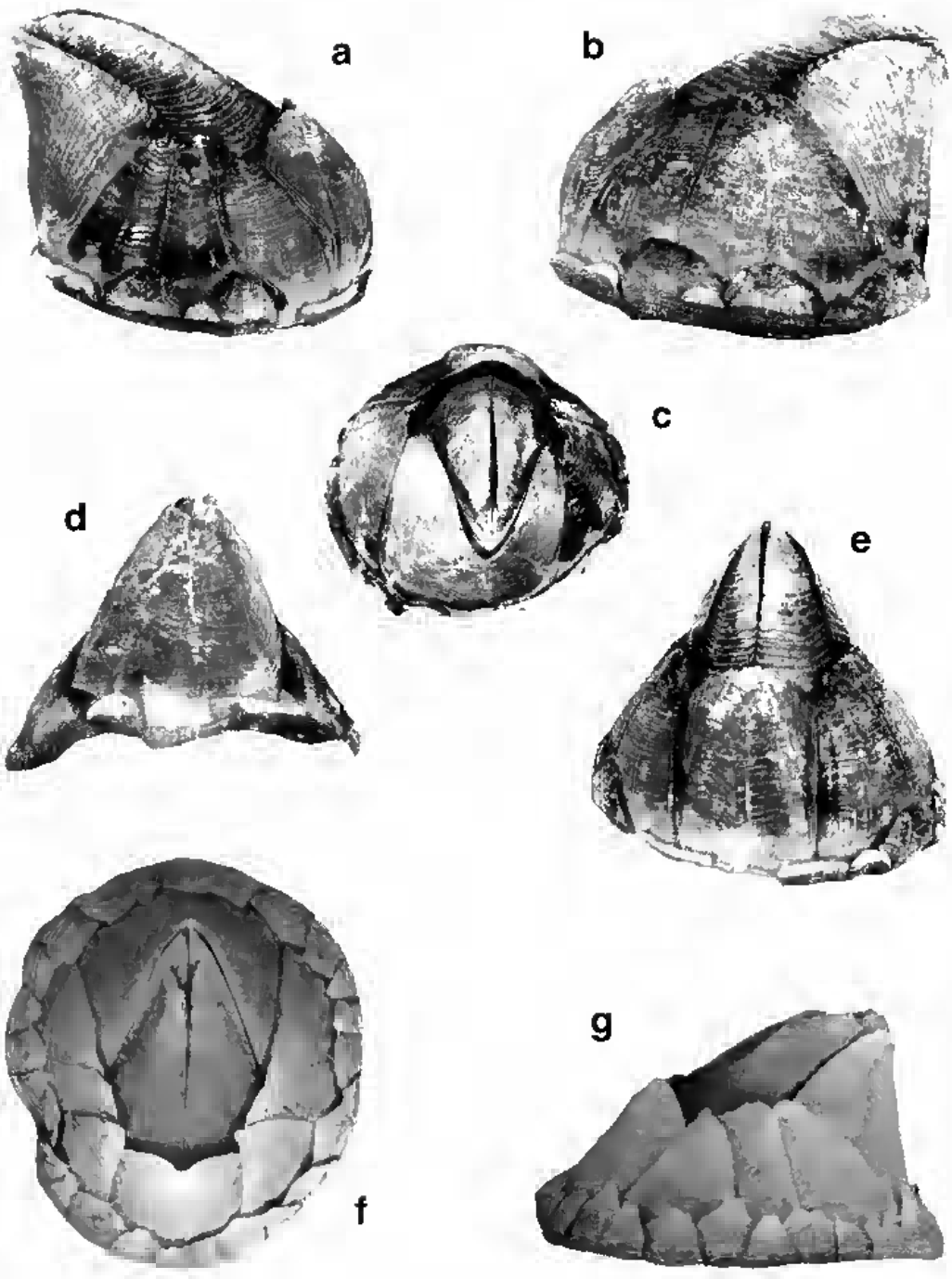

FIG. 2. — *Waikalasma bouchet* n.sp. a-e, holotype, MNHN-Ct2428: a, lateral view of whole specimen (left side); b, lateral view of whole specimen (right side); c, dorsal view of whole specimen; d, carinal view of whole specimen, e, rostral view of whole specimen. f-g, paratype, MNHN-Ct2506: f, dorsal view of whole specimen; g, lateral view of whole specimen (right side). (scale: a-e × 1.74, f-g × 2.17). Photography by P. Lozouet, MNHN, Paris (BIMM).

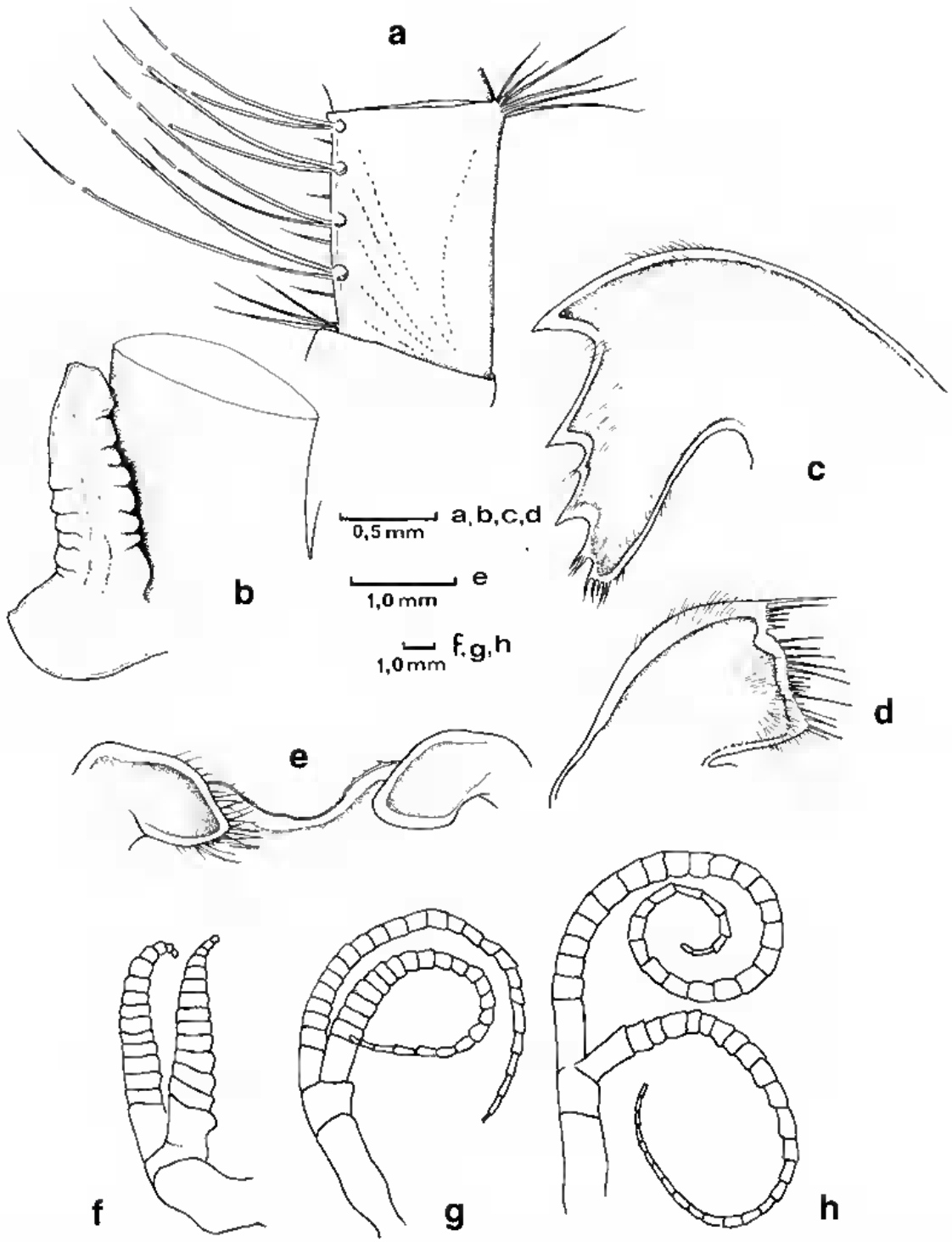

FIG. 3. — *Waikalasma boucheti* n.sp. Holotype, MNHN-Cr2428: a, intermediate segment of cirrus VI showing setal arrangement (right side); b, penis and basal portion of cirrus VI; c, mandible (right side); d, first maxilla (left side); e, labrum and palps (setae shown on left palp only); f, cirrus I (left side); g, cirrus II (left side); h, cirrus III (left side). Cirri I-III shown with setae removed.

plates, and is accepted here. It necessitates considerably fewer imbricating plates than in the reconstruction given in BUCKERIDGE & NEWMAN (1992), and is now much closer to the arrangement seen in *W. boucheti*. Although a very weak medial rib was observed on lateral plates of *W. juneae*, these appear more clearly defined on the living material. The scuta of *W. boucheti* are quite unlike that figured and tentatively attributed to *W. juneae* by BUCKERIDGE (1983: 64). I am now confident that his figure 48 (showing a rather broad valve, with a well formed adductor muscle scar) is not of *W. juneae*, rather, it probably represents another bathylasmatid or a worn balanid scutum. Based on the present reconstruction of *W. juneae* (Fig. 1g), it is clear that the scuta of this species would have been proportionately much shorter than those of *W. boucheti*.

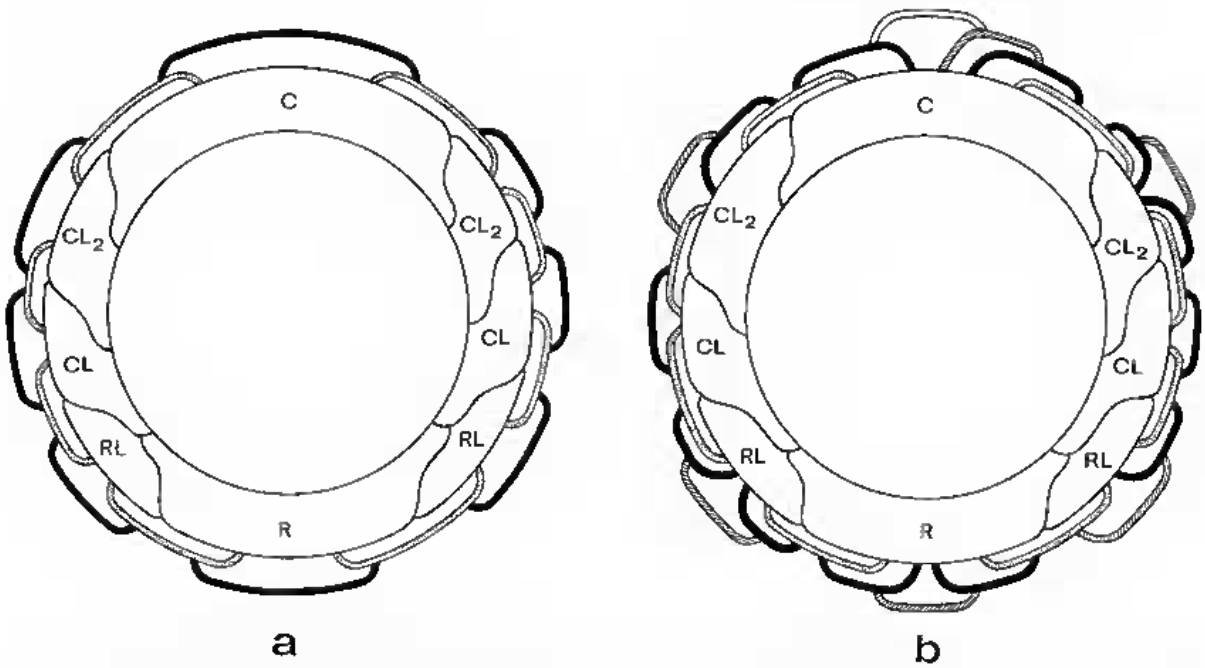

FIG. 4. — *Waikalasma boucheti* n.sp. Schematic plate arrangement (dorsal plans): a, holotype, MNHN-Cl2428, showing inner (stippled) and outer (hatched) whorls, both of eight plates, each overlapping a suture in the inner whorl adjacent; b, paratype, MNHN-Cl2506, showing inner whorl (stippled), of eight plates, each overlapping a suture in the compartmental wall, a second whorl (black), of twelve plates (variously interleaved and overlapping); a third whorl (hatched) of six plates, generally overlapping; a fourth? whorl of one plate, (clear), overlapping plates on second and third whorls. (Note: this diagram demonstrates relationships between plates. It is neither to scale, nor in proportion.). Drawning by J. Rebière, MNHN, Paris (Lab. Zoologie Arthropodes).

AFFINITIES

The number of both compartmental plates and imbricating whorls are sufficient to distinguish this material from *Chionelasmus*, which has a rostrum, carina and four latera in the primary wall, and one whorl of imbricating plates in adults; *Pachylasma* and *Bathylasma* may be differentiated from *Waikalasma* by a lack imbricating whorls. The comparatively larger carina and the intercalation of six lateral plates into the compartmental wall distinguish this genus from

Eochionelasmus. Of the plate structure, the lack of welting in *Waikalasma* places it closer to the Chionelasmatinae than the Pachylasmatinae. As previously noted, the soft parts are quite distinct from *Eochionelasmus*, but as with *Neobrachylepas*, this is likely to be a special trophic adaptation in the latter (YAMAGUCHI & NEWMAN 1990). In general however, the soft parts of *Waikalasma boucheti* are not particularly noteworthy, the maxilla, mandible and labrum are similar to many species within the Pachylasmatinae and Bathylasmatinae, although the absence of caudal appendages distinguishes this genus from *Eochionelasmus*, *Chionelasmus* and *Pachylasma*. Using the absence of characters like caudal appendages in establishing "antiquity" for a group must be approached with caution. If *Waikalasma* is indeed a good candidate as an outgroup for the Pachylasmatinae, and I believe this is so, then it is quite likely that caudal appendages may have been lost some time between the Middle Miocene and the Present, long after the first pachylasmatines appear in the fossil record.

The discovery of *Waikalasma boucheti* n.sp. from the living fauna was quite unexpected. The *Waikalasma* body plan was initially considered as a brief interlude in balanomorph phylogeny (BUCKERIDGE 1983). In this sense *W. boucheti* may truly be viewed as a living fossil. Unlike many other recent and significant discoveries in cirripede phylogeny (*e.g.* NEWMAN 1979, 1985), this material is not associated with a hydrothermal vent environment.

BIOGEOGRAPHY

The Southwest Pacific is confirmed to be of particular significance in sessilian evolution, as 73% of primitive balanomorphs with a generic age older than the Miocene have their earliest records there (BUCKERIDGE 1996). Local endemicity at high taxonomic levels is attributed by NEWMAN (1985) to be either the result of isolation, or association with severe environmental gradients or ecotomes. Although this species is not part of a hydrothermal vent community, such as described by NEWMAN (*loc. cit.*), it is both insular and bathyal, like so many other pachylasmatine and bathylasmatine refugial taxa.

Acknowledgements

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Note added in proof

Since the acceptance of this manuscript for publication, a further incomplete specimen, probably attributable to *Waikalasma boucheti* has been identified by Diana JONES (Western Australian Museum, Perth, Australia), from Loyalty Ridge, Bathus 3, stn DW 778, 24°43'S – 170°07'E, 750-760 m.